Two New Neogene Species and the Evolution of Labral Teeth in *Concholepas* Lamarck, 1801 (Neogastropoda: Muricoidea)

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Abstract. Two new species of *Concholepas* Lamarck, 1801, are described from southern Peru, *Concholepas chirotensis* sp. nov. (middle Miocene) and *Concholepas camerata* sp. nov. (late Pliocene). Both species inhabited high-energy nearshore environments, as have most species of *Concholepas*. The evolution of the genus was most rapid during the late middle Miocene and the late Pliocene, times when the molluscan fauna of the Peruvian Faunal Province experienced mass extinction. A case is made that the late Pliocene development of labral teeth in *Concholepas* was related to changes in prey precipitated by global cooling.

INTRODUCTION

The fossil record of the muricid gastropod genus *Concholepas* Lamarck, 1801, was reviewed recently by DeVries (1995). The known geographic ranges of two Chilean Pliocene species, *C. nodosa* Möricke, 1896, and *C. kieneri* Hupé, 1854, were extended northward to the Pisco and Sacaco Basins of south-central Peru, and the temporal range of the latter species back to the late Miocene. A new early to middle Miocene species from Peru, *C. unguis* DeVries, 1995, was also described. Samples recently collected between Pisco and Camaná (Figure 1) have yielded two new species of *Concholepas*. *C. chirotensis* sp. nov. represents a middle Miocene transition from *C. unguis* to *C. kieneri*. *C. camerata* sp. nov., from upper Pliocene strata, exhibits traits of both *C. kieneri* and the extant *C. concholepas* (Bruguière, 1789), including the two labral teeth of the latter species.

GEOLOGY

Upper Miocene, Pliocene, and Pleistocene marine deposits are widely exposed in the Pisco and Sacaco Basins (Figure 1; Muizon & DeVries, 1985; DeVries, 1998). To the south, lower to middle Miocene bioclastic sandstones of the Camaná Formation surround Camaná (Pecho & Morales, 1969; Ibaraki, 1992). Deposits that unconformably overlie the Camaná Formation were assigned to the upper Miocene Pisco Formation, but the assemblage of mollusks listed by Pecho & Morales (1969) suggests an early to middle Miocene age. Between the Sacaco Basin and Camaná, scattered outcrops of bioclastic sandstone and conglomerate occur along the coast (Olchauski, 1980). Mollusks from these deposits reported by Beaudet et al. (1976) and others found by this author (*Chorus grandis* [Philippi, 1887] and *Acanthina unicornis* [Bruguière, 1789]) indicate a late Pliocene to early Pleistocene age.

Abbreviations used for localities or specimens are as follows:

USNM, Department of Paleobiology, United States National Museum of Natural History, Washington, D.C., USA; L, anterior-posterior Length; W, width at widest point, perpendicular to length; THK, dorso-ventral thickness, measured at widest point.

Material is described with a collections number, locality/sample number, and dimensions (L, W, THK). Measurements enclosed by parentheses indicate sizes for broken specimens. Locality descriptions are given in the appendix.

SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Concholepas* Lamarck, 1801

Concholepas Lamarck, 1801: 69.

Type species (monotypy): *Concholepas peruviana* Lamarck, 1801 (= *Buccinum concholepas* Bruguière, 1789).

Concholepas camerata DeVries, sp. nov.

(Figures 2, 5, 6, 9–11, 14)

Diagnosis: Adults with highly arched body whorl, quadrate aperture; two prominent labral teeth on outer lip.

Description: Shell to 100 mm long, narrow, ovate. Body whorl extending full length of adult shell. Spire submerged. Protoconch not preserved. Body whorl of adults with arched to tabular sutural platform, steeply rounded shoulder, and deeply vaulted mid-section resulting from diminished whorl expansion rate in last quarter to half turn of body whorl. Periphery at midpoint of whorl; anterior longitudinal profile steeply descending to siphonal
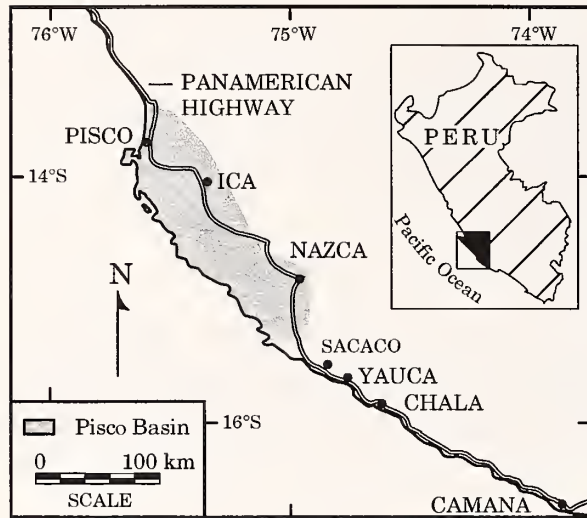
Figure 1

Extent of the Pisco Basin in south-central Peru. The smaller Sacaco Basin extends from a few kilometers north of Sacaco to Yauca. Lower and middle Miocene marine sediments outcrop around Camaná.

notch; no anterior constriction. Juveniles variably inflated. Fasciolar ridge strong; pseudumbilical area dorso-ventrally broad, planar; extending three-quarters length of shell. Aperture quadrate; inner lip slightly reflected outward; columella broad, planar, posterior interior edge bladelike. Posterior end of outer lip inflected at shoulder. Outer lip coarsely crenulate. Spiral sculpture consisting of eight to nine low rounded spiral cords, with one or two secondary cords in most interspaces. Primary spiral cords with irregularly spaced low nodes, sometimes frilled on early whorls where crossed by growth lines. Anteriormost

two interspaces produced and thickened from within outer lip to form two labral teeth.

Discussion: The sculptural pattern of *C. camerata* is unlike that shown by *C. kieneri* (compare Figures 2 and 3) but resembles that of *C. concholepas:* rounded primary spiral cords that are sometimes lamellose; few secondary cords; and two strong labral teeth. The aperture of most specimens of *C. camerata,* however, is more like that of *C. kieneri* (compare Figures 6, 7, and 8): quadrate, not oval; and with a columella whose posterior interior edge is bladelike, not rolled under and thickened, as it is in *C. concholepas;* and an inner lip that is nearly upright, not strongly reflected.

The pattern of whorl expansion for *Concholepas camerata* is intermediate between that seen in *C. kieneri* and *C. concholepas* (compare Figures 11, 12, and 13). In *C. kieneri,* the expansion rate regularly changes, producing a boxlike transverse profile. In *C. camerata,* more rapid juvenile expansion rates are succeeded by lower adult rates, producing a deeply arched transverse profile. In *C. concholepas,* the juvenile expansion rate persists through adult stages, producing a flatter, uniformly convex transverse profile.

A juvenile specimen from locality 95DV 812 (USNM 447126, Figures 9 and 14) exhibits the broad curvature and reflected inner lip of *C. concholepas,* but still retains the shoulder inflection and sharp inner edge at the posterior end of the columella seen in *C. camerata.* Other juvenile specimens from locality 95DV 812 (e.g., USNM 447128, Figures 5 and 10) show the full suite of characteristics diagnostic of *C. camerata.*

Type locality: Locality 95DV 812, south side of Quebrada Huacllaco, roadcut along Panamerican Highway (Figure 21). Specimens of *C. camerata* come from small inliers of sandy coquinas that overlie basement crystalline

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Explanation of Figures 2–20

Figures 2, 5, 6, 9–11, 14. *Concholepas camerata* DeVries, sp. nov. All from sample 95DV 812-1, Quebrada Huacllaco, late Pliocene. 2. USNM 447129, holotype, abapertural view, ×0.7. 5. USNM 447128, paratype, abapertural view, ×1.5. 6. USNM 447129, apertural view, ×0.7. 9. USNM 447126, paratype, abapertural view, ×1.0. 10. USNM 447128, abapertural view, ×1.0. 11. USNM 447129, view from posterior showing transverse profile, ×0.75. 14. USNM 447126, apertural view, ×1.0.

Figures 3, 7, 12. *Concholepas kieneri* Hupé, 1854. USNM 447088, sample 86DV 360-1, South Sacaco, early Pliocene. See DeVries (1995) for more locality data. 3. Abapertural view, ×0.48. 7. Apertural view, ×0.52. 12. View from posterior showing transverse profile, ×0.52.

Figure 4. *Concholepas nodosa* Möricke, 1896. USNM 447122, sample 95DV 809-1, Yauca, early Pliocene, abapertural view, ×1.88.

Figures 8, 13. *Concholepas concholepas* (Bruguière, 1789). Central Peru, Recent. 8. Apertural view, ×0.5. 13. View from posterior showing transverse profile, ×0.50.

Figures 15–19. *Concholepas chirotensis* DeVries, sp. nov. Camaná, middle Miocene. 15. USNM 447120, holotype, sample 95DV 816-1, abapertural view, ×1.0. 16. USNM 447120, apertural view, ×1.0. 17. USNM 447123, sample 95DV 815-1, abapertural view, broken specimen, ×1.0. 18. USNM 447121, paratype, sample 95DV 816-1, abapertural view, ×1.0. 19. USNM 447121, apertural view, ×1.06.

Figure 20. *Concholepas unguis* DeVries, 1995. USNM 447096, holotype, sample 87DV 579-2, near Fundo Santa Rosa, abapertural view, ×1.0. See DeVries (1995) for more locality data.
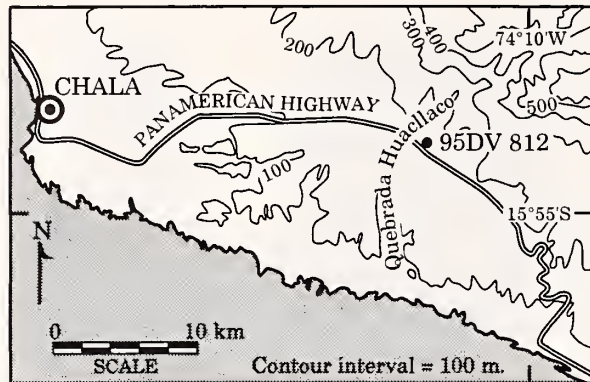
Figure 21

Type locality of *Concholepas camerata* DeVries, sp. nov.

rock at elevations of about 200 to 250 meters above sea level on a narrow wavecut platform.

In addition to specimens from the type locality, specimens of *C. camerata* are also known from upper Pliocene beds in the Sacaco Basin (Localities 96DV 911 and 96DV 923), where they overlie balanid coquinas containing specimens of *C. kieneri* and underlie similar coquinas containing specimens of *C. concholepas.*

Etymology: From the Latin word "camera," meaning "vaulted chamber."

Material: (Sample 95DV 812-1 for all specimens) Holotype USNM 447129, L 79.5 mm, W 56.7 mm, THK 37.1 mm; paratype USNM 447125, L 97.8 mm, W (63) mm, THK (49.4) mm; paratype USNM 447126, L 40.2 mm, W 29.9 mm, THK 12.9 mm; paratype USNM 447127, L 36.0 mm, W (19) mm, THK 14.8 mm; USNM 447128, L 15.5 mm, W 11.4 mm, THK 5.6 mm.

Occurrence: Upper Pliocene, southern Peru.

Concholepas chirotensis DeVries, sp. nov.

(Figures 15–19)

Diagnosis: Shell small, evenly inflated; low spire; pseudumbilical area 60 percent of shell length; surface sculpture of numerous spiral cords, including five to seven nodular primary spiral cords.

Description: Shell small, to 35 mm; ovate, with a large aperture (95 percent of the shell length) and low spire. Spire consisting of two whorls; protoconch unknown. Body whorl without pronounced shoulder; whorls appressed at suture; periphery posterior to midpoint of whorl; anterior quarter of body whorl sometimes weakly constricted. Fasciolar ridge strong, posterior edge with thin keel; pseudumbilical area usually as narrow as fasciolar ridge is wide, extending about 60 percent of shell length. Columella excavated, anterior end flattened, co-
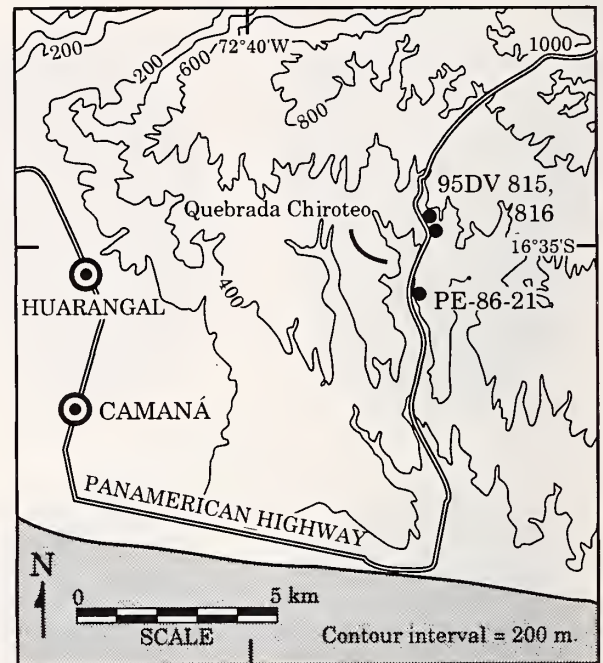

Figure 22

Type locality of *Concholepas chirotensis* DeVries, sp. nov.

planar with aperture; posterior end twisted vertically beneath ridge bordering pseudumbilical region. Inside of outer lip crenulate. Surface sculpture of about 50 spiral cords, including five to seven nodular primary cords, with three to seven secondary cords in interspaces. Numerous evenly spaced growth lines intersecting spiral cords to produce beaded texture.

Discussion: Specimens of *C. chirotensis* have a pseudumbilical area twice as long as that in specimens of the geologically older *C. unguis* and primary spiral cords that are more pronounced and nodular, rather than smooth (compare Figures 15, 17, 18, and 20). Compared with specimens of the geologically younger *C. kieneri,* those of *C. chirotensis* are much smaller, more uniformly inflated, and have many more secondary spiral cords (compare Figures 3, 15, and 17).

Type locality: Locality 95DV 816, Quebrada Chiroteo, 0.5 km east of juncture with Quebrada Mal Paso; roadcut on east side of the Panamerican Highway (Figure 22).

At localities 95DV 815 and 95DV 816, roadcuts expose an irregular granitic basement overlain by cross-bedded coarse-grained sandstones, lenses of gravel with specimens of *C. chirotensis,* laminae of heavy mineral sands, and, basally, rounded and angular cobbles of granite with interspersed large valves of oysters. Two kilometers downhill along the Panamerican Highway, Ibaraki (1992) collected planktonic foraminifera from underlying

strata that yielded an age of late early Miocene (sample Pe-86-21).

In addition to specimens from the type locality, internal molds of *C. chirotensis* are found in bioclastic sandstones overlying volcanic rocks in the northern Pisco Basin (locality 97DV 935). Nearby outcrops of fossiliferous marine sediments in the Filudo Depression have been assigned a middle Miocene age (DeVries, 1998).

Etymology: Named after Quebrada Chiroteo.

Material: Holotype USNM 447120, 95DV 816-1, L 30.9 mm, W 21.0 mm, THK 14.3 mm; paratype USNM 447121, 95DV 816-1, L 24.3 mm, W 17.2 mm, THK 10.3 mm; USNM 447124, 95DV 816-1, six specimens ranging in length from 8.8 to 23.1 mm; USNM 447123, 95DV 815-1, L (38) mm, W 30.7 mm, THK (17) mm.

Occurrence: Middle Miocene, southern Peru.

DISCUSSION

The pattern of evolution for *Concholepas* emerges more clearly with the addition of two species to the four already known (Figure 23)—a pattern of gradual change, followed by two cycles of rapid (punctuated?) change and stasis. From the late early Miocene, by which time *C. unguis* had evolved from a probable non-*Concholepas* species, through the middle Miocene, the size of *Concholepas* shells doubled and the sculpture differentiated into primary and secondary cords (*C. chirotensis*), while coiling remained relatively tight. During the late middle Miocene, coincident with a major molluscan extinction in Peru and Chile, shell size tripled. Whorl expansion became alternatingly rapid and slow in each specimen, producing a dorso-ventrally flattened and quadrate transverse profile (*C. kieneri*). From the late Miocene through the early Pliocene, a time of relative faunal stasis in Peru, the proportions of *C. kieneri* remained unchanged. By the early Pliocene, however, a flattened form had evolved with a flaring aperture and a small number of lamellose primary spiral cords (*C. nodosa*; USNM 447122, Figure 4). By the late Pliocene, another time of mass extinction within the Peruvian molluscan fauna, both dorso-ventrally flattened species were extinct, replaced by populations with toothed shells, quadrate peristomes, and rapid rates of whorl expansion during juvenile stages (*C. camerata*). Toothed individuals with ovate peristomes, reflected inner and outer lips, and rapid rates of whorl expansion at all life stages (*C. concholepas*) appeared by the early Pleistocene.

Four described genera of muricids in the Peruvian Faunal Province are distinguished by labral teeth (DeVries, 1997; DeVries & Vermeij, 1997). Unlike the single labral tooth of the three ocenebrine genera (*Acanthina* Fischer von Waldheim, 1807; *Chorus* Gray, 1847; *Herminespina* DeVries & Vermeij, 1997), which are formed by an infolding and forward projection of the outer shell layer,
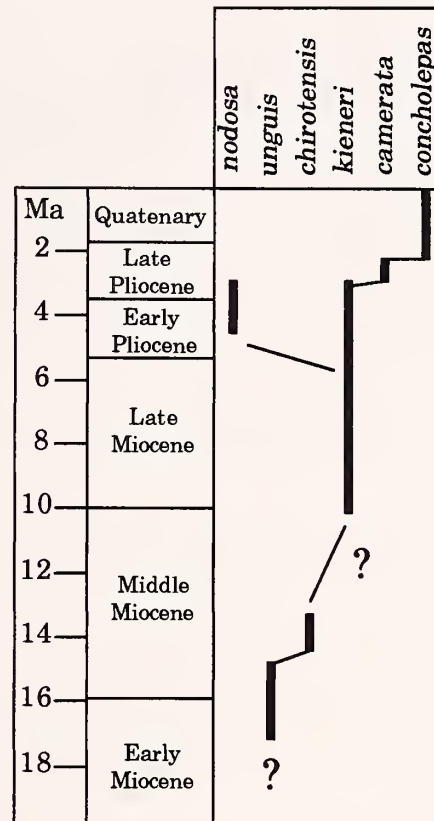

Figure 23

Stratigraphic ranges and inferred phylogeny of *Concholepas*. The taxon ancestral to *C. unguis* remains unknown. An absence of specimens from upper Middle Miocene strata also leaves the nature of the transition from *C. chirotensis* DeVries, sp. nov. to *C. kieneri* in doubt. Ma = millions of years before present.

the paired labral teeth of the rapanine *Concholepas* are thickened, tapered, blunt extensions of the two anteriormost interspaces. The teeth are used during feeding: to brace mytilids while opening them (M. Rabi, personal communication, 1995), to pry apart the integumental plates of barnacles, and to help push and crush ("bulldoze") small barnacles from rocky surfaces (Castilla et al., 1979). The prey favored by *Concholepas* varies with age and location, but includes barnacles (*Balanus laevis* Bruguière, 1789; *B. psittacus* [Molina, 1782]; *Chthalmus cirratus* Darwin, 1854; *C. scabrosus* Darwin, 1854), mytilids (*Perumytilus purpuratus* [Lamarck, 1819] *Semimytilus algosus* [Gould, 1850]; *Brachidontes granulata* [Hanley, 1843]); and the ascidian *Pyura chilensis* Molina, 1782 (Castilla et al., 1979; Dye, 1991; Moreno et al., 1993; DiSalvo & Carriker, 1994).

The transition from untoothed to toothed populations of *Concholepas* is well preserved in a continuous 15-m section of alternating massive sandstones and bioclastic conglomerates on the southeastern flank of the Río Acarí

(Locality 96DV 923). Fossiliferous horizons in the lower 6.2 meters contain species (*Anadara* aff. *A. chilensis* [Philippi, 1887]; *Herminespina saskiae* DeVries & Vermeij, 1997; *Concholepas kieneri*; *C. nodosa*) that indicate an early Pliocene age (Muizon & DeVries, 1985). Coquinas in the uppermost 3 meters contain species (*Glycymeris ovata* [Broderip, 1832]; *Mulinia edulis* [King, 1831]; *Xanthochorus cassidiformis* [Blainville, 1832]; *Concholepas concholepas*; *Oliva peruviana* Lamarck, 1811) that collectively indicate an early Pleistocene age (Muizon & DeVries, 1985). At 9 meters from the base of the section, cobble beds contain the highly arched toothed shells of *Concholepas camerata.* Specimens of *C. kieneri* are still found at 11 m, however, suggesting that populations of *Concholepas* without labral teeth persisted sympatrically for some tens of thousands of years after the toothed species evolved.

Eighty percent of the marine mollusks from southern Peru and Chile, including all that might be considered "tropical," became extinct during the time (3–2 Ma) that toothed populations of *Concholepas* evolved (Herm, 1969; DeVries, unpublished data). This time was characterized by global cooling at middle and high latitudes (Dowsett et al., 1996). As may have been the case elsewhere (Stanley, 1986; Petuch, 1995), decreasing sea surface temperatures in the southeastern Pacific Ocean probably precipitated the mass extinction of Peruvian mollusks.

Concomitant with the mass extinction and evolution of labral teeth in *Concholepas,* the relative abundance of balanid species at Locality 96DV 923 changed. Lower Pliocene strata contain the scuta of *Balanus laevis* and *B. tintinnabulum concinnus* Darwin, 1854. Upper Pliocene strata, seemingly no different in lithology, location, or paleogeographic setting, additionally contain numerous scuta of *B. psittacus.* Unfortunately, no mytilids were found in the Río Acarí deposits, so it cannot be determined if other prey species of *Concholepas* varied in abundance during the same time.

It is instructive to examine the regions from which modern prey species of *Concholepas* were probably recruited during the late Pliocene. Many of the attached rocky intertidal species of the modern Peruvian Faunal Province upon which *Concholepas* preys range well into the cold-water Magellanic Province of southern South America. *Balanus psittacus* ranges from central Peru to the Straits of Magellan (Pilsbry, 1916). *Perumytilus purpuratus* ranges from Ecuador to the Straits of Magellan and north to Santa Cruz, Argentina (Soot-Ryen, 1959). *Brachidontes granulata, Chthalmus scabrosus,* and *Balanus tintinnabulum concinnus* all range as far south as southern Chile (Pilsbry, 1916; Soot-Ryen, 1959). *Semimytilus algosus* ranges from northern Peru only as far south as south-central Chile (Marincovich, 1973), but a southern origin is suggested for this mytilid by its steep decline in numbers when warm water spread along the

coast of Peru during the 1982–1983 El Niño event (Arntz & Tarazona, 1990). In summary, the modern rocky intertidal attached fauna of Peru has a decidedly cold-water cast, more so than the vagrant rocky intertidal fauna or sandy bottom fauna, which have greater proportions of endemic species and immigrant species from warm waters of the Panamic Province.

The following hypothesis is proposed to explain the evolution of the labral teeth in *Concholepas* in a context of the ecological disruption associated with the late Pliocene mass extinction and in light of the modern feeding behavior of *C. concholepas.* Prior to the late Pliocene, less structurally sturdy species of *Concholepas* inhabited the subtidal and lower intertidal zone from southern Peru to central Chile. Individuals of *C. kieneri* and *C. nodosa* probably fed upon a variety of endemic small barnacles and ascidians, as do adults and newly recruited juveniles of *C. concholepas* today (Castilla et al., 1979; Moreno et al., 1993). During the late Pliocene, coastal waters cooled. At the same time, much of the coastal plain of Peru and Chile ceased subsiding and began to rise, producing a coastline that was straighter, rockier, and exposed to higher-energy waves (DeVries, 1985, 1986, 1988). As these changes took place, larvae of mytilids and barnacles swept northward by the Peru-Chile Current from the long-standing rocky shores of southern Chile would have found acceptable substrates for colonization in suitably cool waters. Juvenile individuals of *Concholepas* may have gradually begun feeding upon newly introduced cold-water mytilids and balanids found higher in the intertidal zone, as juveniles do today (Dye, 1991; Moreno et al., 1993). Selection might then have favored arched and corrugated shells with labral teeth capable of dislodging and gripping prey in high-energy intertidal settings. The appearance of labral teeth appears not to be an improbable event in muricids (DeVries & Vermeij, 1997). A single specimen of the early Pliocene *Chorus grandis* (USNM 447074; DeVries, 1997; pl. 2, fig. 6a, b), for example, developed a second, incompletely formed labral tooth anterior to the single fully developed tooth that characterizes all species of the genus.

This evolutionary scenario, in which labral teeth developed in response to changes in prey induced by climate change, could apply equally well to populations of *C. kieneri* from southern Peru or northern Chile. It is conceivable that a Pliocene population of *C. kieneri* in southern Chile might have first evolved labral teeth. Larvae of *C. camerata* might then have been carried north in the Peru Coastal Current together with larvae of cold-water balanids and mytilids. There is no evidence, however, for any Miocene or Pliocene species of *Concholepas* in southern Chile (Hupé, 1854; Philippi, 1887; Herm, 1969; Watters & Fleming, 1972; Tavera, 1979; DeVries et al., 1984; Covacevich & Frassinetti, 1990; Frassinetti, unpublished data on collections from upper Miocene deposits on Isla Mocha, south-central Chile). The occur-

rence of Holocene examples of *C. concholepas* in South Africa (Kensley, 1985) circumstantially suggests that its range has become more extensive at high latitudes following its evolution at lower latitudes.

The hypothesis for the evolution of labral teeth in *Concholepas* can be tested. A careful search for fossil mytilids from rocky intertidal deposits in Peru might reveal their biogeographic history. Quantitative studies of fossil barnacle diversity, biogeography, and predation in Peru and Chile might establish the role of their distribution in the evolution of *Concholepas*. Finally, experimental studies on modern *C. concholepas* could address the adaptive significance of the labral teeth.

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APPENDIX

List of Localities

Locality 95DV 809. Yauca, roadcut on west side of Panamerican Highway as it descends to valley floor; 15°39'49"S, 74°31'50"W (Yauca 1:100,000 quadrangle).

Locality 95DV 812. South side of Quebrada Huacllaco, roadcut along Panamerican Highway (15°52'S, 74°11'W, Chala 1:100,000 quadrangle).

Locality 95DV 815. Quebrada Chiroteo, 0.7 km north of juncture with Quebrada Mal Paso; roadcut on east side of the Panamerican Highway, at an elevation of about 520 m.s.l., 16°34'41"S, 72°37'33"W (Camaná 1:100,000 quadrangle).

Locality 95DV 816. Quebrada Chiroteo, 0.5 km north of juncture with Quebrada Mal Paso; roadcut on east side of the Panamerican Highway, at an elevation of about 500 m.s.l., 16°34'48"S, 72°37'32"W (Camaná 1:100,000 quadrangle).

Locality 96DV 911. Acarí Depression, 6 km north-northeast of Chaviña, southeastern base of ridge extending eastward into depression, 15°34'37"S, 74°36'20"W (Yauca 1:100,000 quadrangle).

Locality 96DV 923. About 0.5 km southeast Monte Redondo, east side Río Acarí, ridge inside shallow, small depression, 15°36'29"S, 74°37'53"W (Yauca 1:100,000 quadrangle).

Locality 97DV 935. Northwest side of Cerro Antivo, south of road between Pozo Santo and Laguna Grande, at pass southwest of Cerro El Diablo. Inlier of bioclastic sandstone and gravel. 14°03'49"S, 76°08'58"W (Punta Grande 1:100,000 quadrangle).